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Land snail diversity in subtropical rainforest mountains (Yungas) of Tucumán, northwestern Argentina

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Abstract: A survey of the micro-land snails in the mountain rainforest or "Yungas" of Tucumán Province, Northwestern Argentina (26°20′-27°30′S) was carried out. A total of 75 samples were processed from 25 stations of 10 × 10 m each. We identified the snails collected to species level and built a species per station data matrix to analyze patterns of diversity. Non-parametric estimators (ICE and Chao2) using EstimateS 5.0.1 were used to estimate the true diversity of the area, the degree of undersampling, and spatial aggregation in the data. Other diversity measurements such as Shannon and Whittaker indices were also calculated. Our study estimated the micro-mollusc species richness of the Yungas of Tucumán to be 21 species distributed among 9 families, with a notably high number of specimens collected (7741). The most speciose family was Charopidae with a total of seven species identified. However, the most abundant families were Diplommatinidae and Systrophiidae. *Adelopoma tucma* and *Wayampia trochilioneides* were the most abundant species, the least frequently found species was *Lilloiconcha tucumana*. The non-parametric estimators showed that our survey was complete and that patchiness did not affect diversity estimations. San Javier and Escaba stations had the highest species richness, the most diverse station was Escaba. Most previous studies in other places in the world show high species richness and low density of specimens. In Tucumán, on the contrary, the absolute abundance of specimens was high with a low species richness.

Key words: Species richness, micro-molluscs, taxonomy, *Adelopoma*, South America

The subtropical mountain rainforest or "Yungas" in northwestern Argentina ranges from 300 to 2000 m above sea level, in areas where it rains more than 1000 mm annually (Brown and Grau 1995). Grassland areas distributed above 1800-2000 m are often included in this ecoregion, although they have a completely different kind of vegetation from that characteristic of the Yungas. The Yungas, together with the rainforest of the Paranaense region (Northeastern Argentina), represents less than 2% of the surface of Argentina but contains more than 50% of the biodiversity present in this country. The Yungas, also known in Argentina as "Tucumano-Boliviano" rainforest, are latitudinally distributed along a narrow area in the northwestern part of the country from the boundary with Bolivia (S 22°) to southern Catamarca province (S 28°). One of the reasons for the comparatively high diversity of flora and fauna reported in the Yungas is the marked altitudinal variation that occurs in this region. The flora comprises three well differentiated altitudinal zones having distinct physiognomies and floras.

Huge areas of the Tucumano-Boliviano rainforest were already degraded or profoundly altered before basic information on biodiversity, including a complete inventory of molluscan species, could be obtained. Detailed data on diversity of undisturbed forest faunas are therefore urgently needed. Our lack of knowledge on biodiversity is particularly apparent concerning invertebrate taxa, especially land molluscs (de Winter and Gittenberger 1998, Myers *et al.* 2000). The micro-snails are poorly studied in most forest regions of South America. This situation is worsened because specimen representation of the local fauna in malacological collections is also inadequate, due to the limited funds available for taxonomic studies (Wheeler 2004). Limited taxonomic and ecological information of most land snail groups distributed in South America make it almost impossible to incorporate this group of invertebrates into plans of conservation (Myers *et al.* 2000, Lydeard *et al.* 2004). One of the present prejudices is the statement that land snails are neither diverse nor abundant in ecosystems like tropical and subtropical rainforests due to their type of soil and weather (Solem 1984). Solem stated that the lack of nutrients and litter and the abundance of predators on the molluscan fauna make the tropical rainforest an unfavorable habitat for snails. On the contrary, other environments with stable temperatures, moderate moisture, and rich soil litter are habitats with the highest diverse land snail faunas. Several studies around the world (in Madagascar [Emberton 1995, Emberton *et al.* 1996, 1999], Mexico [Naranjo and García 1997], French Guyana [Gargominy and Ripken 1998], Cameroon [de Winter and Gittenberger 1998], Kenya [Tattersfield *et al.* 2001], and Venezuela [Martínez 2003]) have tried to test Solem's hypothesis with respect to the environmental conditions. Most of them concluded that in fact tropical rainforests can contain very speciose gastropod faunas. Nevertheless, very little information for comparisons exists with respect to subtropical rainforest areas, where the floral composition, weather conditions, seasonality, and type of soil differs considerably from tropical areas. Moreover, a progressive decline in richness and abundance of characteristic tropical land snail groups inhabiting northern and central South America (*e.g.*, Systrophiidae, Streptaxidae, Neocyclotidae) towards lower latitudes and the eventual replacement of these groups by others inhabiting southern subtropical rainforest habitats is a process not clearly documented nor understood. It is also not clear if the decline of species richness along a latitudinal gradient proposed for vertebrates is also valid for most invertebrates including land molluscs but excluding arthropods (Longino *et al.* 2002). Even if this latitudinal gradient in South America would also be valid for land snails, the causes in the changes of species richness and species turnover have not yet been hypothesized.

This study aimed to: (1) Determine the taxonomic composition of the micro-molluscan fauna from the Yungas in Tucumán, (2) Establish the species richness (gamma diversity) of this ecoregion, which is the result of the alpha (within community) and beta (variation of species composition among communities) diversities, and (3) Compare these results with the species richnesses and abundances reported for other parts of the world, especially the southern hemisphere.

MATERIALS AND METHODS

Study area

Our field research was carried out in the biogeographic region of the Yungas or Tucumano-Boliviano rainforest in Tucumán Province, northwestern Argentina (26°15′-27°40′S). This area corresponds to the southernmost extension of the Andean Neotropical Montane Forest (Cabrera 1971, Cabrera and Willink 1973). Precipitation in the Yungas is characterized by a monsoonal regime with rainfall concentrated in the summer and early autumn months (November-April) (Grau and Veblen 2000). The Yungas ecoregion is usually divided into three altitudinal vegetation zones (Brown and Grau 1995, Valdora and Soria 1999). The Piedmont Forest located from 400 to 700 m above sea level consists of the basal portion of the Yungas, with an annual precipitation of about 600 to 1000 mm. It is also called "Transition rainforest" (Cabrera 1971, Prado 1995). It is mainly characterized by deciduous trees and a low abundance of epiphytic vegetation. Some of the most common trees are *Tipuana tipu* (Benth, 1898) (common name: "tipa"), *Enterolobium contortisiliquum* (Vellozo, 1892) ("pacará"), *Phoebe porphyria* (Grisebach, 1889) ("laurel"). The degradation process (*e.g.*, over explotation, fires, crops) produced great structural transformation of the piedmont rainforest into xerophilic woods (Brown and Grau 1995). This basal zone of the Yungas is the most affected by human activity in Tucumán. The Lower Montane Forest extends from 700 to 1500 m, with an annual precipitation between 1500 and 3000 mm. Some of the most characteristic trees of this altitudinal zone are *Tipuana tipu* (Beth, 1898) ("tipa"), *Jacaranda mimosifolia* Don, 1822 ("tarco"), *Phoebe porphyria* (Grisebach, 1889) ("laurel"), *Myrcianthes uniflora* (Linné, 1773) ("arrayán") and *Blepharocalyx gigantea* Lillo, 1911("horco molle"). Above 1500 m is the Upper Montane Forest, with an annual precipitation between 900 and 1300 mm. This zone is characterized by the presence of *Podocarpus parlatorei* Pilger, 1903 ("pino del cerro"), and *Alnus acuminata* (Kunth, 1904) ("aliso").

Sampling

The material used in the present study consisted of adult terrestrial micro-molluscs from different taxonomic groups. Micro-molluscs or micro-snails are defined as those species that as adult have shells not larger than 5 mm maximum dimensions. Molluscs larger than 5 mm, informally called macro-molluscs, were not considered in the present study because they were too low in abundance and patchily distributed to be adequately sampled by our methods. Thus we excluded *Epiphragmophora* Doering, 1874, *Scutalus* Albers, 1850, *Drymaeus* Albers, 1850, and specimens of Veronicellidae. All of the specimens of micro-snails collected were deposited at the Fundación Miguel Lillo Malacological Collection, Tucumán, Argentina. The methodology used in the present study was adapted from those of Emberton *et al.* (1996) and de Winter and Gittenberger (1998). We sampled 25 stations consisting of a 10 × 10 m patch during the summer season when land snails are more active in Tucumán Province (Fig. 1, Table 1). Within each station we qualitatively searched for micro-snails for half an hour in selected microhabitats that seemed the most favorable for them, such as between exposed roots of trees where dead organic material usually accumulates and under and between dead tree trunks lying on the forest floor. In each station we also took three samples of 50 × 50 cm quadrats of leaf litter plus 2 cm of topsoil from moist, sheltered microhabitats so that a total of 75 samples were processed from the total of 25 stations. Because land snails are generally distributed in patches, it seemed more appropriate to take samples from places most suitable for them. For each station we recorded the altitude (Thommen altimeter), latitude and longitude (Garmin GPS), general topography, and kind of vegetation. Leaf litter plus topsoil samples were placed in plastic bags and kept as cool as possible (10-15°C) in the laboratory no longer than one week until processing. Each bag was opened daily for

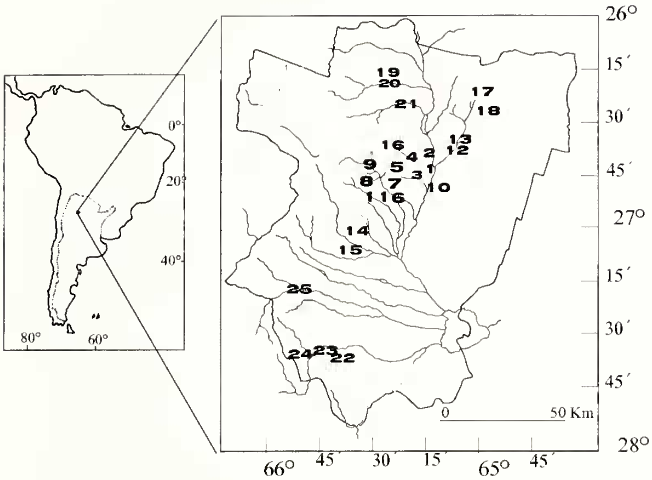

Figure 1. Map of Tucumán province indicating the 25 sample stations located in 15 geographic localities. Station numbers correspond to those listed in Table 1.

aeration. The qualitative search provided more living specimens in most of the stations than did the soil plus leaf litter samples. All snails found alive were relaxed in deoxygenated water for 24 hours and then preserved in 90% ethanol. Soil plus leaf litter samples were dry-sieved through three decreasing mesh widths (3 mm, 1.5 mm, and 0.5 mm) in the laboratory. The three samples from the same station search were treated together for the statistical analysis because there were no differences in the species composition nor in the abundance of specimens among them. After the process of separation of soil and snails, shells were sorted and identified using a Leica MZ6 stereoscopic microscope. An altitudinal transect from 800 to 1460 m was carried out in the Sierra de San Javier locality (Stations 1-5). In this transect the stations (five in total) were sampled every 100 m of elevation to estimate the possible altitudinal variation of the community in the different vegetation zones of Yungas.

Taxonomic identification

Specimens were identified based on shell characters only, except in the case of *Wayampia trochilioneides*

Table 1. Stations (Sn) sampled for micro-molluscs in Tucumán. T_s = total number of species collected per station. T_{ind} = total number of specimens collected per station. PF = Piedmont Forest, LM = Lower Montane Forest, TF = Transition Forest, UM = Upper Montane Forest.

SN #	Name	Elevation (m)	Latitude S	Longitude W	Rainfall (mm/year)	T_s	T_{ind}	Type of vegetation
1	Nina's road, San Javier Mountain	920	26°43′11″	65°17′35″	1505	14	565	PF
2	Nina's road, San Javier Mountain	1020	26°43′07″	65°18′02″	1505	14	289	LM
3	Nina's road, San Javier Mountain	1120	26°43′11″	65°18′17″	1505	14	688	LM
4	Nina's road, San Javier Mountain	1210	26°43′09″	65°18′33″	1505	14	386	LM
5	Nina's road, San Javier Mountain	1460	26°42′54″	65°18′47″	1505	7	15	UM
6	Horco Molle, Yerba Buena Dept.	940	26°51′32″	65°25′32″	1500-2000	11	211	PF
7	Estancia San Javier, Tafi Viejo Dept.	1050	26°46′26″	65°23′24″	1173	12	173	LM
8	Potrero de Las Tablas, Lules Dept.	750	26°46′16″	65°25′34″	1083	11	809	PF
9	Potrero de Las Tablas, Lules Dept.	800	26°46′16″	65°25′34″	1083	9	115	PF
10	San Miguel de Tucumán, Capital	450	26°48′26″	65°14′58″	986	4	82	PF
11	Raco, La Hoyada	880	26°46′16″	65°28′04″	694	11	270	LM
12	El Cadillal, Aguas Chiquitas	515	26°36′48″	65°11′11″	1096	13	352	PF
13	El Cadillal, Aguas Chiquitas	560	26°36′51″	65°11′11″	1096	12	362	PF
14	Tafi del Valle	550	27°05′43″	65°37′10″	900	7	138	PF
15	Tafi del Valle	900	27°03′22″	65°40′20″	800-1000	10	148	LM
16	Villa Nougues	1200	—	—	1173	7	55	LM
17	Medinas Mountain, Buruyacu Dept.	1200	—	—	—	4	141	LM
18	Timbó Viejo, Burruyacu Dept.		26°26′28″	64°59′43″	—	7	245	TF
19	Gonzalo, San Pedro de Colalao	1250	26°18′40″	65°31′45″	600-800	9	445	LM
20	Hualinchay, Trancas Dept.	1360	26°19′35″	65°2′21″	700-900	10	687	LM
21	Rearte, Trancas	1370	26°21′05″	65°32′25″		5	16	TF
22	Escaba abajo, Juan Bautista Alberdi	600	27°38′57″	65°44′46″	1119	10	88	PF
23	Escaba abajo, Juan Bautista Alberdi	650	27°40′02″	65°45′40″	1119	13	681	PF to LM
24	Escaba arriba, Juan Bautista Alberdi	700	27°39′14″	65°46′11″	1119	12	491	PF to LM
25	Cochuna	1235	27°19′41″	65°55′33″	1400-1600	10	253	LM

(d'Orbigny, 1835), for which anatomical dissections were also used. Only specimens with complete shells were considered. Some shells from species difficult to identify were mounted on stubs, sputter coated, and observed with a Jeol 35CF scanning electron microscope. We identified the material collected to species level and built a species per station data matrix to analyze patterns of diversity. For the taxonomic identification we used the available regional identification keys (Fernández and Castellanos 1973) plus the original species descriptions. We followed the general classification for Neotropical micro-molluscs of Muller da Fonseca and Thome (1993) and a general classification of Gastropoda by Wade *et al.* (2001).

Diversity measurements

To estimate the true number of species in the community, we used non-parametric estimators of diversity calculated with EstimateS, version 5.0.1 (Colwell 1997). EstimateS uses the relative abundance of rare species to estimate the number of species not seen. EstimateS was also employed to assess the degree of undersampling and spatial aggregation in the data. This program computes randomized species accumulation curves and reports the means of various statistics based on those curves (Heyer *et al.* 1999). A species-accumulation curve is a plot of the accumulated number of species found with respect to the number of units of effort expended. In the present study, the effort is of a discrete-type (samples). The species-accumulation curve for a highly undersampled fauna will appear nearly linear, with each sample adding many new species to the inventory. On the contrary, the curve for a thoroughly sampled fauna will reach a plateau, with few or no species being added with additional sampling (Longino 2000). We treated the data as presence and absence scores of species by samples. The estimator chosen in the present study for non-parametric richness estimation were the Incidence-based Coverage Estimator (ICE) (Lee and Chao 1994) and the Chao2 estimator (Chao 1987). Relying on the concept that rare species carry the most information about the number of missing ones, Chao uses only singletons and doubletons to estimate the number of missing species. When the abundance-based coverage estimators (ACE) were used, transforming the former matrix by adding the abundance of each taxon per sample, similar curves were obtained. We used the default values for number of randomizations (50) and cutoff values for coverage-based estimators (10). Both estimators, ICE and Chao2, augment the negatively biased observed richness by a factor that depends on the presence of and distribution within samples of "rare" taxa. For the estimator used, the "rare" species are those observed in only one or two samples (ICE is more complex but the logic is the same). When all species in the data matrix had been observed multiple times, the inventory is complete but when inventories are replete with "rare" species, true richness is underestimated. EstimateS 5.0.1 include techniques to assess graphically the degree of spatial aggregation in the data. For this purpose a Coleman curve (rarefaction curve) was also calculated (Fig. 2). Coleman curves are not estimators of species richness in the same sense as the other estimators. While Chao2 and ICE estimate total species richness, rarefaction curves estimate sample species richness from the pooled total species richness (Colwell 1997). Rarefaction curves represent the means of repeated re-sampling of all pooled samples.

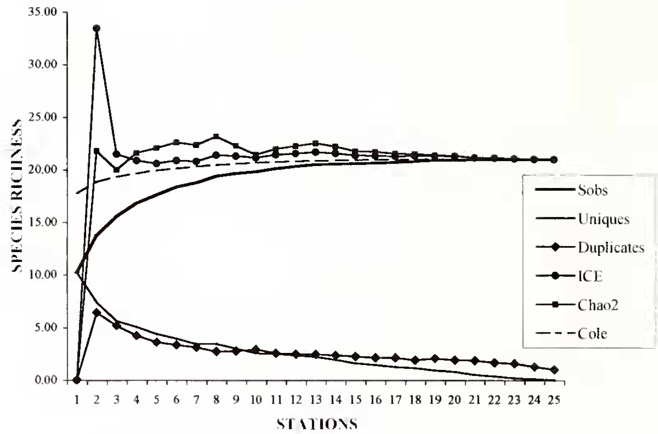

Figure 2. Species richness estimators and patchiness indicators for the micro-snails of the Yungas in Tucumán. Species accumulation curves and Coleman curves obtained with EstimateS 5.0.1.

Other diversity indices used in this work were the Shannon Index, Evenness Index and the Whittaker Index. The Shannon Index (H′) determines the alpha (α) diversity obtained through the equation:

$$H' = -\sum p_i \log_2 p_i$$

Where p_i= proportion of individuals in the i^{th} species (ni/N) (Magurrán 1989). Evenness (E) was calculated using the formula:

$$E = H'/H_{max}$$

Its value fluctuated between 0 and 1. An E=1 means that all of the species present at the station are equally abundant (Magurrán 1989). To estimate beta (ß) diversity we used the Whittaker index (I):

$$I = (S/\alpha) - 1$$

which consist of the total number of species (S) divided by the mean number of species per station (α) (Whittaker 1975, Magurran 1989, de Winter and Gittenberger 1998). The Whittaker index provides a measurement of the variability among sites (= stations). The community that contributes with fewer species will have the highest β diversity. If I is equal to 1, then the stations have the same or identical faunas and higher values indicate increasing differentiation (de Winter and Gittemberg 1998). The Whittaker index does not take into account the distribution of species on spatial or environmental gradients, so this index is not intended to be used to measure species turnover (Vellend 2001). The total number of specimens recovered per station (each station of 100 m^2) was used as an estimate of abundance.

RESULTS

Faunal composition

In the present study, we found 7741 specimens representing 21 species in 15 genera and 9 families, one of them was a "prosobranch" and the remaining were pulmonates (Table 2). The total species per stations data matrix is given in Table 3. The most speciose family was Charopidae, with a total of seven species recorded. Following Charopidae, were Pupillidae (3 species) and Systrophiidae (3 species). The three families together represented 62% of the total number of species. The rest of the families were represented by lower numbers of species, generally one or two. Of the total number of families represented, only one is carnivorous, the rest are herbivorous or detritivorous. The species richness per station ranged from 4 to 14 species (Table 1). The richest stations, with 14 species recorded, were between 1000 m and 1200 m of elevation in the San Javier mountains (Tables 1, 3). These stations were located in the biological reserve of the National University of Tucumán, a protected area called Parque Sierra de San Javier.

Density fluctuated between 16 and 809 specimens per 100 m^2 (Table 3). The densest station was Potrero de Las Tablas with 809 specimens in 100 m^2 located at 750 m. Abundance of specimens was low in those stations that had a substrate with sand, or with a high proportion of small stones and that were more exposed to sunlight. The most common and abundant taxa were *Adelopoma tucma* Doering, 1884 and *Wayampia trochilioneides* (d'Orbigny, 1835). Some species of the genus *Radiodiscus* Pilsbry, 1906 were also very abundant, especially in stations from San Javier Mountain (Tables 1, 3). The micro-molluscan fauna was dominated by two families, Systrophiidae and Diplommatinidae, that were present in 24 out of 25 stations sampled, although the number of genera represented in each of these families was low in the study region. Individuals of *W. trochilioneides* were absent only in stations 10 and 17 corresponding to San Miguel de Tucumán city and Medinas (Tables 1, 3). Station 10 had an environment modified by human activities, where invasive species (*Zonitoides arboreous* [Say, 1816], *Opeas pumilum* [Pfeiffer, 1840]) were more frequent than native ones. Station 17 was a dry transition forest habitat with a low frequency of occurrence of several species that typically inhabit humid forests. Individuals of *A. tucma* were very abundant in humid habitats of low montane forest, especially when those habitats were well preserved, as at stations 1-4. When the conditions of the forests

Table 2. Systematic classification of the species collected at the 25 stations sampled in the Yungas of Tucumán. Classification systems according to Wade *et al.* (2001) and Muller da Fonseca and Thome (1993).

CLASS GASTROPODA
SUBCLASS PULMONATA
ORDER EUPULMONATA
- SUBORDER STYLOMMATOPHORA
- INFRAORDER ORTHURETHRA
- FAMILY PUPILLIDAE
  - *Pupisoma latens* Hylton Scott, 1960
  - *Pupisoma dioscoricola* (Adams, 1845)
  - *Gastrocopta pulvinata* Hylton Scott, 1948
- INFRAORDER SIGMURETHRA
- FAMILY CHAROPIDAE
  - SUBFAMILY ROTADISCINAE
    - *Radioconus pilsbryi* (Hylton Scott, 1957)
    - *Radioconus crenulatus* (Hylton Scott, 1963)
    - *Radiodiscus wygodzinskyi* Weyrauch, 1965
    - *Radiodiscus katiae* Hylton Scott, 1948
    - *Radiodiscus golbachi* Weyrauch, 1965
    - *Trochogyra gorduraensis* (Thiele, 1927)
  - SUBFAMILY AMPHIDOXINAE
    - *Ptychodon amancaezensis* (Hidalgo, 1869)
- FAMILY HELICODISCIDAE
    - *Lilloiconcha tucumana* (Hylton Scott, 1963)
- FAMILY FERUSACCIIDAE
  - *Caecilioides consobrina* (d'Orbigny, 1835)
- FAMILY SYSTROPHIIDAE
  - *Wayampia trochilioneides* (d'Orbigny, 1835)
  - *Drepanostomella tucma* Hylton Scott, 1948
  - *Miradiscops* sp.
- FAMILY ZONITIDAE
  - *Zonitoides arboreus* (Say, 1916)
  - *Zonitoides nitidus* (Müller, 1774)
- FAMILY EUCONULIDAE
  - *Guppya lilloana* Hylton Scott, 1948
  - *Guppya aenea* Hylton Scott, 1948
- FAMILY SUBULINIDAE
  - *Opeas pumilum* (Pfeiffer, 1840)

SUBCLASS "PROSOBRANCHIA"
ORDER CAENOGASTROPODA
- SUBORDER ARCHITAENIOGLOSSA

SUPERFAMILY CYCLOPHOROIDEA
- FAMILY DIPLOMMATINIDAE
  - *Adelopoma tucma* Doering, 1884

showed some alteration or had secondary vegetation, *A. tucma* was notably less common or was completely absent. The species *Guppya aenea* (Hylton Scott, 1948) had a high frequency of occurrence (96%) in the stations, being absent only in Medinas (station 17), but the congeneric *Guppya lilloana* (Hylton Scott, 1948) occurred with less frequency (84%). Among the less frequently occurring taxa was *Lilloiconcha tucumana* Hylton Scott, 1963 (12%) found only in piedmont forest and in low montane forest of San Javier. It was absent in all the other locations. *Opeas pumilum* (Pfeiffer, 1840), *Z. arboreous* and *Zonitoides nitidus* (Müller, 1774) were found in localities with high human activities, such as Tucumán City, Villa Nougues, and El Cadillal stations.

Table 3. Data matrix of the species collected and the stations sampled and used in the analysis.

SPECIES/ STATIONS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Radioconus pilsbryi	0	1	0	16	14	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0
Radiodiscus crenulatus	2	0	3	2	11	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	10	8	3
Radiodiscus wygodzinskyi	55	86	240	146	0	1	0	37	4	0	3	30	9	0	14	0	0	19	0	0	0	0	0	0	4
Trochogyra gorduraensis	8	1	79	16	0	18	0	0	18	0	0	1	0	0	0	4	6	0	0	0	0	0	14	2	4
Ptychodon amancaezensis	1	6	5	2	0	28	5	0	0	0	1	0	6	6	0	0	7	4	88	138	4	0	30	40	2
Radiodiscus golbachi	0	0	0	2	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Lilloiconcha tucumana	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Radiodiscus katiae	20	15	13	16	5	4	0	0	0	0	3	10	26	0	6	0	0	0	189	139	5	14	40	35	0
Cecilioides consobrina	7	13	0	0	0	0	4	17	0	0	9	55	30	5	8	0	0	0	0	0	0	10	37	11	0
Zonitoides arboreus	1	0	0	0	0	0	13	0	0	1	0	44	0	11	0	1	113	0	0	0	0	0	0	0	0
Zonitoides nitidus	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pupisoma latens	7	5	5	2	0	1	1	3	11	0	1	12	14	0	2	1	0	0	19	31	0	14	52	31	15
Pupisoma dioscoricola	0	0	0	0	0	0	0	0	0	0	0	0	14	0	5	0	0	13	0	0	0	3	19	0	0
Gastrocopta pulvinata	0	0	0	0	0	0	0	5	0	0	9	6	7	0	0	0	0	0	12	11	0	2	1	33	0
Wayampia trochilioneides	104	46	105	31	9	57	42	249	25	0	67	55	92	63	26	29	0	146	102	288	5	5	50	67	63
Miradiscops sp.	32	70	26	21	5	20	28	31	10	0	21	9	0	1	3	0	0	0	4	9	0	8	16	10	52
Dreponostomella tucma	1	2	2	6	0	20	3	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0
Guppya lilloana	10	2	18	5	4	23	2	10	8	0	1	11	50	10	6	0	0	1	4	8	1	8	8	8	0
Guppya aenea	27	12	60	20	3	35	4	34	32	11	9	31	109	42	4	3	0	27	25	27	1	14	40	55	2
Adelopoma tucma	290	29	131	101	0	4	67	420	6	15	146	87	2	0	74	16	0	35	0	34	0	10	364	191	105
Opeas pumilium	0	0	0	0	0	0	2	0	0	55	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
TOTAL	565	289	688	386	51	211	173	809	115	82	270	352	362	138	148	55	141	245	445	687	16	88	681	491	253
Mean number of specimens per station	27	14	33	18	2.4	10	8.2	39	5.4	3.9	13	17	17	6.5	7	2.6	6.7	12	21	33	0.7	4.1	32	23	12

Table 4. Calculated values of the Shannon index (H′), Whittaker index (*I*), and Evenness for each sampled station.

STATIONS	H′	*I*	Evenness
1	2.3097	0.50	0.6066
2	2.7856	0.50	0.7316
3	2.6649	0.50	0.7202
4	2.6817	0.50	0.7043
5	2.6163	2.00	0.932
6	2.9126	0.90	0.8419
7	2.4355	0.75	0.704
8	1.883	0.90	0.5668
9	2.7591	1.33	0.8704
10	1.175	4.25	0.7413
11	2.3091	0.90	0.6441
12	3.0736	0.61	0.8306
13	2.7911	0.75	0.7786
14	2.0256	2.00	0.7215
15	2.3689	1.10	0.7131
16	1.8242	2.00	0.6498
17	1.0877	4.25	0.5044
18	1.8369	2.00	0.6543
19	2.1997	1.30	0.6939
20	2.334	1.10	0.7026
21	2.0488	3.20	0.8824
22	3.1332	1.10	0.9432
23	2.5152	0.61	0.6797
24	2.8186	0.75	0.7862
25	2.1881	1.10	0.6587

In the altitudinal transect between 800 and 1460 m of elevation in the San Javier Mountains, the species richness and composition of the micro-snail community between piedmont and low montane forest were the same. A sharp decrease in the number of species (from 14 to 7) was detected between low montane and upper montane forest. Density was also low in the upper montane forest.

Diversity estimators and diversity index

The behavior of ICE and Chao2 estimators with respect to the accumulation species curve (Sobs) is shown in Fig. 2. The gap between richness estimators and the observed species accumulation curve was very narrow. The curves converged, becoming flat with increasing numbers of samples. Both Chao2 and ICE estimators estimated 21 species, which closely approximated the observed species accumulation curve at the sample number 20. The behavior of the "rare" species curves (uniques and duplicates) was typical of a complete inventory (Heyer *et al.* 1999). When the number of stations was low the curve for the unique species rose faster than did the curve for duplicate species. With increasing numbers of stations, both declined, crossing and tending towards zero when no species remained to be discovered and almost all species were known from two or more localities. In the present analysis the calculated Coleman curve nearly followed the observed curve, showing no evidence of patchiness.

The diversity values obtained using the Shannon index fluctuated from 1.08-3.13 (Table 4). The most diverse stations were in the Escaba area (H′ = 3.13; E = 0.94) (station 22) and El Cadillal (H′ = 3.07; E = 0.83) (station 12). The stations with lowest diversities were Medinas (H′ = 1; E = 0.50) (station 17) and San Miguel de Tucumán city (H′ = 1.17; E = 0.74) (station 10).

The values calculated for the Evenness Index (E) ranged from 0.56 to 0.94 (Table 4). These high values close to 1 mean that those stations were not very different in species abundance. The stations richest in species (stations 2-4, each with 14 species recorded) had similar high values of evenness (0.70-0.73), meaning that in each of these stations the species were close to be equally abundant.

The Whittaker index (*I*) fluctuated between 0.50 and 4.25 with an average of 1.46 (Table 4). This high value indicated a substantial degree of beta diversity or differentiation among stations.

DISCUSSION

We recorded the presence of 21 species of micromolluscs from stations in the Yungas area in northwestern Argentina. Comparisons of species richness with previous works worldwide are difficult to make because most of them had considered macro- and micro-molluscs together and applied different methodologies. Some of the studies carried out in the southern hemisphere reported the highest levels of species richness in the world. Barker and Mayhill (1999) reported the presence of 105 species of terrestrial molluscs within the Pukeamaru District in New Zealand, de Winter and Gittenberger (1998) reported 97 species of land snails in a square kilometer of rainforest in Cameroon and in Madagascan rainforests, 80 species of micromolluscs in 20 × 20 m patches were found by Emberton *et al.* (1996), and 61 species were found in a square kilometer in Malaysian Borneo (Schilthuizen and Rutjes 2001). The North American land snail fauna is relatively well studied (Lydeard *et al.* 2004). Emberton (1995) reported that the most diverse site is located on Pine Mountain, Kentucky, U.S.A., which has yielded 44 species of land gastropods in four hectares. In Central and South America, several lists of taxa from restricted geographical localities are available in some countries but research on diversity of land gastropods are very scarce. In consequence, diversity is probably seriously underestimated. In Mexico, a total of 52 species have been reported from tropical rain forest leaf litter in southern Veracruz (Naranjo-García 1997), 34 species from a km^2 of forest in French Guyana (Gargominy and Ripken 1998), and in the Camisea region, Perú, 49 species have been also found (Ramírez *et al.* 1999). Unfortunately, countries like Bolivia or Colombia with a high biodiversity have been poorly inventoried for land snails.

Although the species richness recorded for Tucumán in the present study is low (21 species of micro-snails) in comparison with other previously studied sites in the southern hemisphere, the total number of specimens collected was very high (7741 micro-molluscs specimens). Density in our study (specimens in a 10 × 10m station) ranged from 16 to 809 and varied altitudinally. In comparison, Emberton *et al.* (1999), working in southeast areas (total of 0.04 ha) of Madagascar, found a total of 2430 specimens from 80 micromolluscan species. Densities (specimens in a 20 × 20 m plot) in their study ranged from 20 to 104. In the present study, species richness and density declined with increasing altitude along a transect carried out in San Javier Mountains. The highest density in Tucumán was found in Potrero de Las Tablas, a piedmont forest station.

The most speciose family of the micro-mollusc fauna in Tucumán is Charopidae with 7 species represented in the area from a total of 26 species of the same family reported for Argentina (Fernández 1973). Charopidae is the dominant and most speciose family of other faunas of the southern hemisphere, such as the Pukeamaru fauna in New Zealand. Barker and Mayhill (1999) found 56 species of Charopidae in that area, a notably higher species richness compared to Tucumán. One of the dominant families in our study was Systrophiidae, with three species represented in Tucumán out of 8 species of this family reported for Argentina (Fernández 1973). In northern areas of South America, the Systrophiidae were found to be one of the predominant families, as is the case in Camisea, Perú, with 14 species reported in that study area (Ramirez *et al.* 1999) from a total of 55 species cited for the whole country (Ramirez *et al.* 2003). On the contrary, the family Charopidae (25 species reported for Argentina [Fernández 1973]) seems to be more abundant in southern South America than in Perú (13 species reported [Ramírez *et al.* 2003]). Studies on distribution, species richness, and systematic classification of Charopidae from South America are still scarce. Many families that are common and abundant in northern South America are not present or are poorly represented in southern South America. Similarly, another carnivorous family, the Streptaxidae, which is very abundant and diverse in northern South America, is scarce in southern areas of South America.

Adelopoma tucma Doering, 1884, one of the most common species in the Yungas, was very abundant in the richest stations of this study, with specimens numbers ranging from 105 to 420 in stations with 10 to 14 species (the highest species number recorded in a station). This species is very abundant in well preserved forests between 600 and 1200 m of elevation that had low human impact. This species was less common or is completely absent in places where the substratum and vegetation were altered by human activity. This was apparent in stations 1-4 from the San Javier protected area that has a low human impact compared with the other stations. A second highly abundant species was *Wayampa trochilioneides* (d'Orbigny, 1835), whose number of specimens was high at the same stations as *A. tucma.* In areas of piedmont forest with anthropogenic alterations, some non-indigenous species from the genera *Opeas* Albers, 1860 and *Zonitoides* Lehmann, 1862 were present. Of the indigenous fauna, the less frequently found species were *Lilloiconcha tucumana* Hylton Scott, 1963 (Helicodiscidae), which was found in only two stations, and *Radiodiscus golbachi* Weyrauch, 1965 (Charopidae), found in three stations. On the contrary, the most frequently found species of the indigenous fauna was *Guppya aenea* (Hylton Scott, 1948), which was found in 24 stations.

According to our study, the inventory was found to be complete by the non-parametric estimators of diversity used, which are particularly suitable for small samples (Colwell and Coddington 1994). These results indicated that with further collecting effort in this area no other species would probably be found. Historical records for Tucumán province, mainly from malacological collections, show the presence of additional species of micromolluscs, such as *Zilchogyra hyltonscottae* Weyrauch, 1965 and *Radiodiscus thomei* Weyrauch, 1965 (Charopidae). These two species were not found in our study area, perhaps because species of Charopidae inhabiting South America are not well described. Taxonomic revisions are urgently needed, in part to test the validity of nominal species. For instance, *Radiodiscus thomei* Weyrauch, 1965 and *Radiodiscus katiae* Hylton Scott, 1948, are extremely similar and original descriptions do not provide unique characters for each species. A revision of the genus is necessary to resolve these taxonomic issues.

The Coleman curve closely followed the observed species-accumulation curve, indicating that aggregation in the data was not affecting estimates of species richness. The true diversity of micro-snails in the Yungas of Tucumán was estimated to be 21 species, with a high abundance of specimens.

The β diversity calculated with the Whittaker index had a high mean value of 1.46. This suggests substantial differentiation in species composition among the stations (Barker and Mayhill 1999). The richest stations, such as those in San Javier (1-4 in Fig. 1, Table 1) had similar Whittaker indices (0.5), but station 5 from the upper montane forest of San Javier that had a low species richness, had a high value of the Whittaker index (2), meaning that there was difference in diversity of the fauna present in this last station in comparison with the others. Stations with high Whittaker indices, have low species richness (Magurrán 1989) and, in this case, were the ones with more human pressure (*e.g.*, stations 10, 17).

The α diversity, the diversity in each station/community, calculated with the Shannon index, showed the highest values at El Cadillal (station 12) and Escaba (station 22). These values were similar to the ones obtained in some stations of the Pukeamaru area in New Zealand (Barker and Mayhill 1999). However, values obtained with the Shannon index are difficult to compare with other places because of the different methodology employed and area considered.

Land snail faunas of tropical rainforest tend to be quite diverse (Emberton *et al.* 1996). Much of this diversity is a consequence of the micro-molluscan fauna. Because most South American rainforests are largely undercollected for micro-land snails and are undergoing significant deforestation, there is an urgent need to collect and study the molluscan fauna. In solving the present biodiversity crisis, taxonomic work remains an essential tool. Revisionary taxonomy is frequently dismissed as merely descriptive, which belies its strong intellectual content and hypothesis-driven nature (Wheeler 2004). Diversity studies on South American molluscan fauna as well as systematic revisions of land molluscs are urgently needed and must be developed, especially in countries where high biodiversity occurs.

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